38. On the Myology and Classification of the Wombat, Koala, and Phalangers. By Charles F. Sonntag, M.D., F.Z.S., Anatomist to the Society.

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(Text-figures 31–43.)

Contents.

Introduction.

The most remarkable features in the existing classifications of the Diprotodont Marsupials* are the positions assigned to the Wombat, Koala, and Phalangers. Some zoologists have included the Koala in the Phalangeridæ and kept the Wombat separate. Others have included the Koala and Wombat in the Phascolarctidæ. And others again have formed three families—Phalangeridæ, Phascolarctidæ, and Phascolomyidæ. It is evident, therefore, that there is considerable difference of opinion as to the true positions of these animals. To form a lasting and natural classification one must examine all anatomical data, so as to exclude convergent and adaptive characters, and those which represent varying degrees of persistence of primitive conditions which were present in their common ancestor. The exclusion of these conditions, leaves us with data which are of value for purposes of classification. And these can be divided into major and minor groups. Minor characters are employed to emphasise the classification based on major ones.

In the examination of animals received at the Society's Prosectorium † I observed so many points in their myology hitherto unrecorded, or different from existing accounts, that I have considered it fit to set them down as a separate section in this paper. As the anatomy of the skeleton, teeth and viscera is already well known I have simply mentioned the most distinctive characters in the section on classification.

Myology.

Muscles of the Head and Neck.

The *Platysma* in all species is muscular in the face and neck. It is continuous with the facial, orbital, and auricular muscles,

* Pocock (**9**) and Osgood (**7**) have reproduced most of the systems of classification which have been proposed.

† *Phascolomys mitchelli* (♂ ♀), *Phascolarctos cinereus* (♀), *Phalanger orientalis* (adult female and female mammary fœtus), *Pseudochirus peregrinus* (♀ ♀ ♀). Many points in the anatomy of *Trichosurus vulpecula* have been described by me in a former paper (**10**).

but the fusion is best marked in *Phascolarctos*. Fibres run to the pads of vibrissæ, but none are continuous with the well-developed muscles in the labial labrets in *Phascolomys*. There is no essential point of difference between the platysma in these forms and the Phalangeridæ.

Masseter:—The general form is similar in *Phascolomys* (text-fig. 31 A) and *Phascolarctos* * ; in the former the anterior border is thick and muscular, but it is thin and tendinous in the latter. In *Phalanger* (text-fig. 31 B) and *Pseudochirus* (text-fig. 31 C) the form differs from the above: in the former the surface is subdivided by sulci into three parts, but it is undivided in the latter.

Pterygoids:—Macalister (**5**) observed that the external pterygoid is small and fused with the internal pterygoid in *Phascolarctos*, but I found it separated and well developed in all forms.

Digastric (text-figs. 32–34 †):—In *Phascolarctos* it is monogastric and fused with the mylo-hyoid, genio-hyoid, and omo-hyoid; and it is inserted into the mandible. I have already shown that it enters into a sheet with mylo-hyoid and sterno-hyoid (**10**), and I believe that the lateral fibres of the sheet correspond to the digastric. Young (**14**) described two bellies and a tendinous inscription. In *Phascolomys* the broad anterior bellies conceal the mylo-hyoid, and strong intermediate tendons unite them to the posterior bellies. In *Phalanger* the broad anterior bellies do not completely cover the mylo-hyoid, and the posterior bellies are fusiform. In *Pseudochirus* the monogastric muscles conceal the greater part of the mylo-hyoid. In no species has the digastric any connection to the hyoid bone. There is, therefore, a close resemblance between the digastric muscles in *Phascolarctos* and *Pseudochirus*.

Mylo-hyoid (text-figs. 32–34, M-H.M):—In *Phascolomys* and the Phalangers the mylo-hyoid runs from the mandible to the hyoid bone. But in *Phascolarctos* it does not get any attachment to the hyoid. In my specimen it is fused with the sterno-hyoid; and there is, in reality, a sterno-mandibularis. Young (**14**) does not mention fusion of mylo-hyoid and sterno-hyoid, but notes that the mylo-hyoid has no attachment to the hyoid bone.

Omo-hyoid (text-figs. 32–34, O-H.M):—In *Phascolomys* and the Phalangers it is attached to the hyoid bone, but no central tendon is present. In *Phascolarctos*, however, it avoids the hyoid bone and passes forwards to enter the tongue, wherein it forms a lingualis.

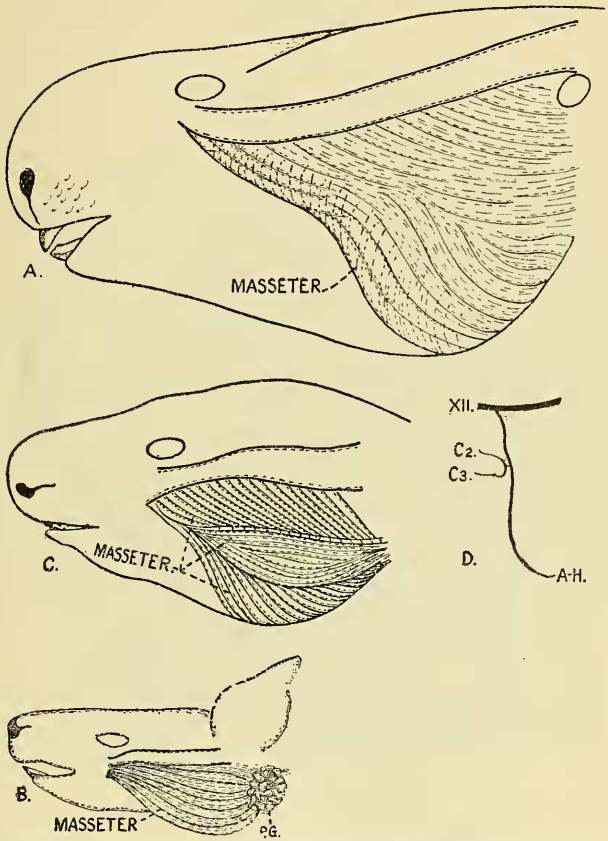
The ansa hypoglossi, which supplies the omo-hyoid and pretracheal muscles, is derived from the cervical plexus alone in *Phascolarctos*, *Phascolomys*, and *Pseudochirus*. In *Phalanger* I observed the nerve receiving connections from the first three cervical and the hypoglossal nerves (text-fig. 31 D).

* P. Z. S. 1921, p. 548, text-fig. 53.

† *Ibid.*, p. 549, text-fig. 54.

Pretracheal Muscles:—In all the animals described in this paper the sterno-hyoid muscles could easily be separated from the subjacent sterno-thyroids. The sterno-hyoids are fused in *Phascolarctos* and have no connection to the hyoid bone, so they

Text-figure 31.



The masseter muscle in *Phascolomys mitchelli* (A.), *Pseudochirus peregrinus* (B.), and *Phalanger orientalis* (C.); D: the ansa hypoglossi in *Phalanger orientalis*.

C2 and C3: cervical nerves; A-H: ansa hypoglossi; P.G: parotid glands XII: hypoglossal nerve.

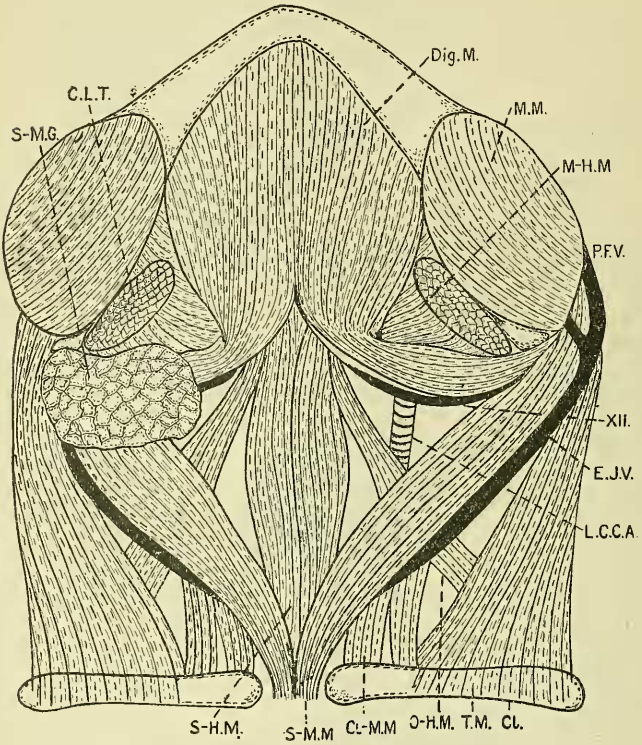
play no part in its movements. But in all other species they are separate and receive an insertion to the hyoid. The sterno-thyroids are essentially similar in all.

Hyoglossus:—Young (**14**) describes it as a transverse band, bridging over the genio-glossi, and having no hyoid attachment

in *Phascolarctos*. I did not, however, observe this band at all. Macalister (5) regarded it as a piece of the mylo-hyoid. In *Phascolomys* and the Phalangers it runs from the hyoid bone to the tongue.

It is, therefore, evident that the Koala has many traces of

Text-figure 32.



Anatomy of the neck in *Phascolomys mitchelli*.

CL: clavicle; CL-M.M: cleido-mastoid; C.L.T: cervical thymus; Dig.M: digastric; E.J.V: external jugular vein; L.C.C.A: left common carotid artery; M-H.M: mylo-hyoid; M.M: masseter; O-H.M: omo-hyoid; P.F.V: posterior facial vein; S-H.M: sterno-hyoid; S-M.G: submaxillary gland; S-M.M: sterno-mastoid; T.M: trapezius; XII: hypoglossal nerve.

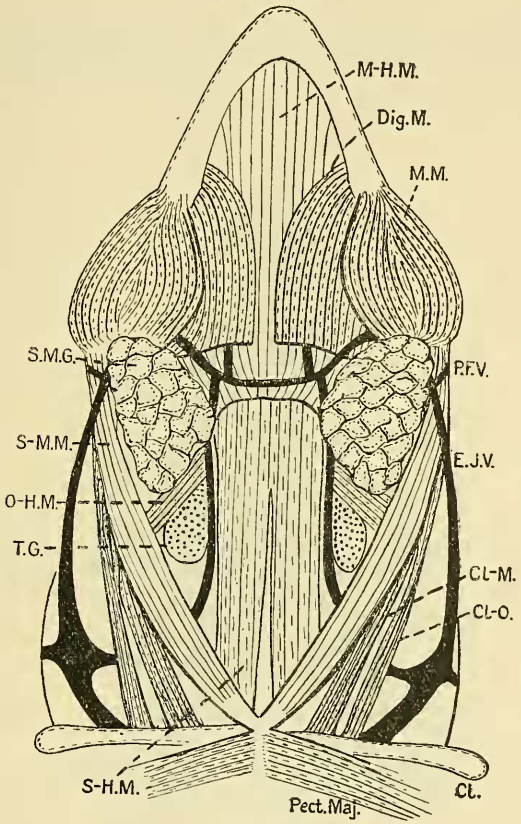
primitive lamination in its platysma, mylo-hyoid, sterno-hyoid, and hyoglossus muscles. And in these conditions it differs entirely from *Phascolomys* and the Phalangers.

Sterno-mastoid, *Cleido-mastoid*, *Cleido-occipital* (text-fig. 32, S-M. M, Cl-M, Cl-O):—All are present in the Phalangers, but the

last is absent in *Phascolarctos* and *Phascolomys*. The insertion of sterno-mastoid and cleido-mastoid is into the occipital crest.

Genio-hyoid :—In my specimen of *Phascolarctos* it runs from the symphysis of the mandible to the hyoid bone and thyroid cartilage, so it is in reality a genio-hyo-thyroid. This arrangement

Text-figure 33.



Anatomy of the neck in *Phalanger orientalis* (adult).

CL-O : cleido-occipital ; Pect.Maj : pectoralis major ; T.G : thyroid gland. Other letters as in last figure. In a mammary fœtus the cervical thymus concealed the lower part of the neck. Note the vertical anterior jugular veins and the horizontal vena transversa.

differs from Young's account (**14**). As no other thyro-hyoid muscles are present, they are probably replaced by a part of the genio-hyoid.

The genio-hyoids and stylo-hyoids are the only muscles

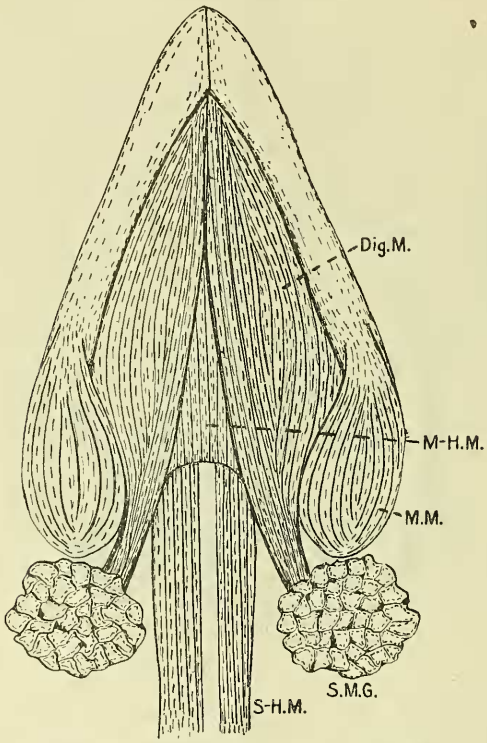
attached to the hyoid bone in my specimen of *Phascolarctos*, for the pharyngeal constrictors have no hyoid origin.

Scaleni:—In all forms the scalenus anticus is absent, as the scalene group is behind the brachial plexus. The scalenus medius and posticus are present.

Splenius:—In *Phascolarctos* it is divisible into two parts (capitis and colli), but it is a single sheet in *Phascolomys* and the Phalangers.

Prevertebral Muscles:—Young (14) described these muscles in *Phascolarctos*, and pointed out that they are more or less

Text-figure 34.



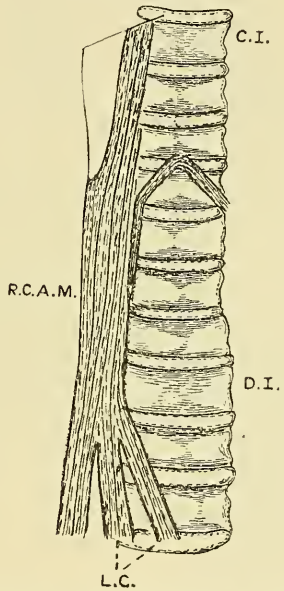
Anatomy of the neck in *Pseudochirus peregrinus*.

Letters as in text-fig. 32.

inseparable. The rectus capitis anticus major is the largest; it runs from the bodies of the first three dorsal vertebræ and all cervical transverse processes to the basi-occiput. Rectus capitis anticus minor cannot be isolated. Longus colli consists of fibres running between the bodies and transverse processes of the first

three dorsal and cervical vertebræ. In *Phascolomys* I observed similar fusion of these muscles. A single thick muscular sheet extends from the third dorsal vertebra to the basi-occiput (text-fig. 35). A small bundle of fibres becomes detached, and runs to the front of the third cervical vertebra when it fuses with the bundle from the opposite muscle. The main mass, in my opinion, represents rectus capitis anticus major. The mesial part represents longus colli, and the rectus capitis anticus minor is absent. In *Phalanger* there is more separation between the longus colli and rectus capitis anticus major, and there is no rectus capitis anticus minor. But in *Pseudochirus* there is considerable

Text-figure 35.



Prevertebral muscles in *Phascolomys mitchelli*.

Letters in text.

fusion. It appears, therefore, that the conditions in *Phalanger* do not adhere so much to the primitive condition as do those in *Phascolarctos*, *Phascolomys*, and *Pseudochirus*.

Muscles of the Back, Thorax, and Abdomen.

Trapezius :—In all forms the origin extends from the occiput to the seventh dorsal spine, although Young (14) gave the eighth spine as well in *Phascolarctos*. The clavicular insertion varies, however. In *Phascolarctos* and *Pseudochirus* most of the fibres go to the clavicle, but some cross it and run to the clavicular deltoid,

In *Phascolomys*, on the other hand, most of the fibres cross the clavicle and fuse with the clavicular deltoid; and some fuse with the cleido-mastoid. In *Phalanger* the conditions are intermediate. The scapular insertion is, however, similar in all. And in no case is there a tendinous intersection where the fibres cross the clavicle. The fusion of the trapezius and clavicular deltoid is a persistence of the primitive lamination, and is best marked in *Phascolomys*.

Rhomboideus:—In all forms it is an indivisible sheet whose origin extends from the occiput anteriorly to the thoracic region posteriorly, and it thickens from before backwards. It reaches the fifth dorsal spine in *Phascolomys*, but stops at the third in *Phascolarctos*, *Phalanger*, and *Pseudochirus*. As the rhomboideus shows no division in any of these animals they all exhibit a persistence of the primitive condition of the muscle.

Latissimus Dorsi:—This muscle arises from a variable number of posterior thoracic spines and the lumbar fascia, but there are neither iliac nor scapular origins. Costal slips may exist. The following origins were present in my specimens:—

Phascolarctos: spines 4–10; no costal origin.
Phalanger: spines 4–12; slip from last rib.
Pseudochirus: spines 4–12; no costal origin.
Phascolomys: spines 5–15; slips from lower six ribs.

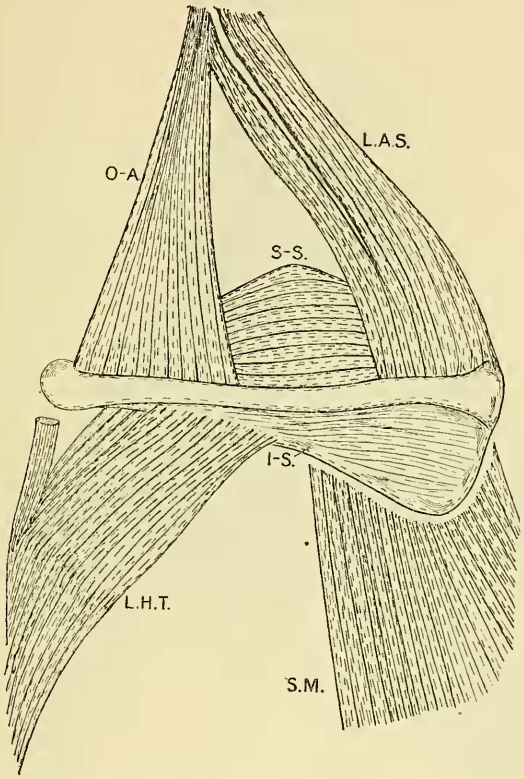
The insertion of the latissimus is very similar in all, and it is intimately connected to the teres major and dorso-epitrochlearis.

Levator Anguli Scapulæ:—Young (**14**) states that it arises from the front of the lateral mass of the atlas along with the first slip of the serratus magnus in *Phascolarctos*; but he does not mention whether it is fused with the omo-atlantic. It is inserted into the scapular spine. In *Phascolomys* I observed it arising in company with the omo-atlantic from the caudal border of the lateral mass (text-fig. 36 A). And it is closely connected to the upper part of the serratus magnus. It is attached to the root of the spine of the scapula. In *Phalanger* (text-fig. 37) it arises in common with the omo-atlantic, but is separate from the serratus magnus. It is inserted into the dorsal surface of the scapula in the anterior part of the supraspinous fossa. In *Pseudochirus*, on the other hand, it is inseparable from the serratus magnus, and its insertion never reaches the spine of the scapula. It is, therefore, evident that *Phascolomys* and *Phascolarctos* differ from the Phalangers in the insertion of the levator scapulæ. So the conditions of the levator scapulæ and serratus magnus are degrees of persistence of primitive lamination.

Omo-atlantic (text-figs. 36 & 37):—In *Phascolomys* and *Phascolarctos* it runs, widening as it goes, from the lateral mass of the atlas to the outer part of the spine of the scapula. And the lateral fibres cover the dorsal part of the shoulder joint. In *Phalanger* and *Pseudochirus* it divides into two parts—a broad mesial and a narrow lateral slip—and these are attached to the

outer half of the scapular spine. Cunningham (2) describes it as two muscles fixed to the whole length of the scapular spine in *Cuscus*. The conditions in the Phalangers cannot be due to their leading an active arboreal life, as other active animals have a single muscle. They are probably remnants of primitive laminations.

Text-figure 36.



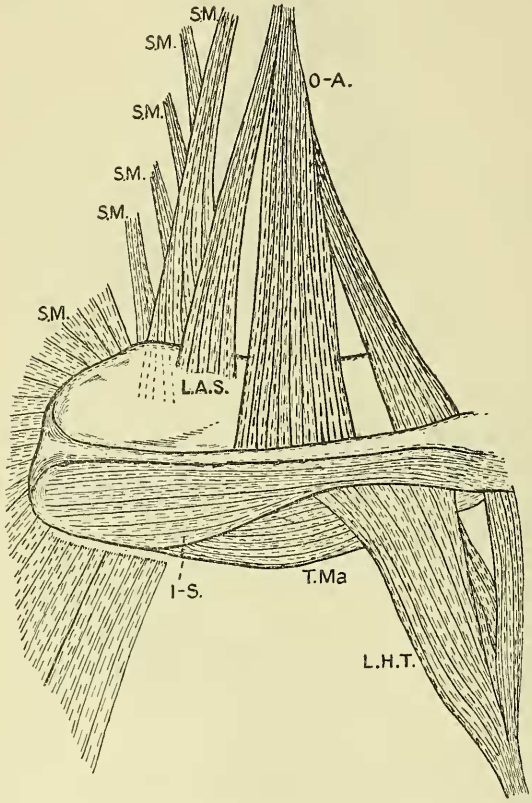
Scapular muscles in *Phascolomys mitchelli*.

I-S: infra-spinatus; L.A.S: levator anguli scapulæ; L.H.T: long head of triceps; O-A: omo-atlantic; S.M: serratus magnus; S-S: supra-spinatus.

Serratus Magnus (text-figs. 36–38):—In the Marsupialia there is a more or less intimate connection between the levator scapulæ and the serratus magnus, thus showing that these muscles are part of the same sheet. And the origin of the serratus extends from the anterior cervical to the posterior thoracic region. In *Phalanger* the origin extends from the second cervical vertebra to the seventh rib. The cervical slips are all distinct. In *Pseudochirus* there are eight thoracic slips. The cervical slips are

also coarser than the thoracic ones, but they are closer together. In *Phascolarctos* Young (**14**) described six cervical and nine thoracic slips, and I observed the same. But Macalister (**5**) recorded seven costal slips. As regards *Phascolomys*, Macalister pointed out that the cervical and thoracic parts are separate, and he described them in detail.

Text-figure 37.



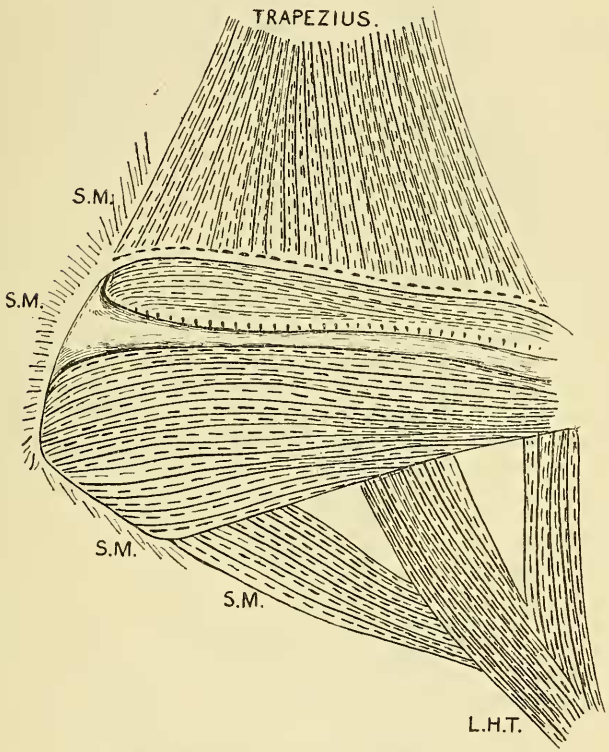
Scapular muscles in *Phalanger orientalis*.
T.Ma : teres major. Other letters as in text-fig. 36.

Intercostal Muscles:—The number of sets of intercostals varies, as the result of variations in the number of ribs, but the characters of the muscles are essentially similar in all :—

Phascolarctos: ten pairs of interspaces.
Phascolomys: fourteen pairs of interspaces.
Phalangeridæ ; twelve pairs of interspaces.

Muscles of the Ventral Abdominal Wall:—In the Phalangers at my disposal the muscles of the ventral abdominal wall were all firmly united together and the linea alba was very obvious. The rectus abdominis had eight intersections, and the first one was so wide that there is apparently a rectus abdominis and rectus thoracis. This condition was also present in Young's specimen of *Phascolarctos* (**14**). In *Phascolarctos* and *Phalanger* the pyramidalis conceals the rectus, and gets one insertion into the sternum

Text-figure 38.



Scapular muscles in *Phascolarctos cinereus*.
Letters as in text-fig. 36.

and last costal cartilage, but it is not so extensive in *Phascolomys*. These animals are, however, essentially similar as regards all the muscles of the ventral abdominal wall.

Dorsal Abdominal Muscles:—The quadratus lumborum is well developed in *Phascolomys* and the Phalangers. In *Phascolarctos* it is more primitive, for it is practically absent, or, as Young (**14**) suggests, it may be replaced by intertransverse muscles connecting

the lumbar vertebræ. The psoas parvus exceeds the magnus in all forms, but the disproportion is not so great, and the parvus is more tendinous in *Phascolomys*. Macalister (18) describes it as a weak muscle in the latter. It is inserted into the pubis behind the corresponding marsupial bone in all forms.

Muscles of the Anterior Extremity.

The *Dorso-epitrochlearis* arises from the posterior border of the latissimus dorsi and its tendon in *Phalanger* and *Pseudochirus*, and it remains muscular to its insertion into the tip and inner border of the olecranon. In *Phascolarctos* it is thin, and a considerable part is fascial. In *Phascolomys* it arises chiefly from the tendon of the latissimus, and it is firmly bound down by deep fascia. When the fore-limb is abducted the muscle becomes tight soonest in the latter. And the distant extremity is more evidently continuous with the anconeus internus in *Phascolarctos*.

Pectoral Muscles:—Cunningham (2) analysed the pectoral mass, and described a pectoralis major composed of superficial and deep parts, a pectoralis minor, and a pectoralis quartus. In my specimens the conditions present differed in some respects from those described by Young, Cunningham, Macalister, and others.

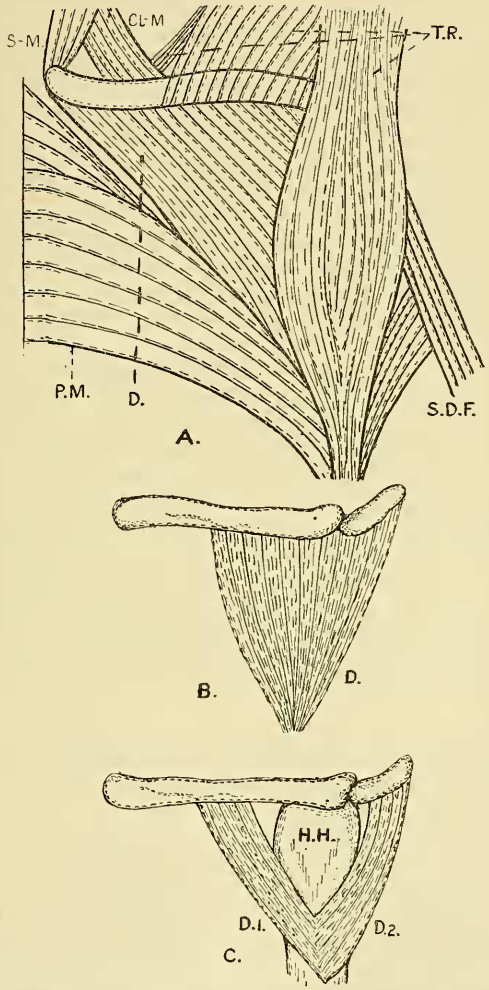
Pectoralis Major:—In *Phascolomys* Macalister (18) showed that the superficial part has clavicular, sternal, and costal origins. In my specimen (text-fig. 39 A) it arises from the mid-sternal line and fascia over the abdominal muscles in the infra-sternal fossa; there is no clavicular nor costal origin. It is inserted into the pectoral crest of the humerus and fuses extensively with the clavicular deltoid. The deep part arises from the manubrium sterni, crosses the pectoralis minor and quartus, and is inserted by a narrow tendon into the outer tuberosity and upper part of the pectoral crest. It is separated from the first part. In *Phalanger* the superficial part does not arise from the entire length of the sternum, but in other respects it resembles the superficial part in *Phascolomys*. The deep part has a more extensive origin from the body of the sternum. In *Pseudochirus* the conditions are similar to those in *Phalanger*, but it is difficult to distinguish the superficial part from the clavicular deltoid in the fused muscular mass. In *Phascolarctos* the superficial part has an origin from the inner third of the clavicle, so the clavicular deltoid does not reach the sterno-clavicular joint as it does in *Phascolomys*. I have already described and figured muscles resembling those in the latter in *Mandrillus leucophæus*.

Pectoralis Minor:—In *Phascolomys* it arises from the posterior three-fourths of the sternum, and it is inserted into the great tuberosity, coraco-humeral ligament, and coracoid process. It remains separate from the quartus, but their insertions are contiguous. In *Pseudochirus* the minor and quartus are in contact throughout the greater part of their course. But in *Phalanger* and *Phascolarctos* they are separate.

Subclavius:—The insertion varies. In *Phalanger* it is attached

to the outer two-thirds of the anterior border of the clavicle. In *Pseudochirus* the conditions are similar to the above. In

Text-figure 39.



Clavicular muscles in *Phascolomys mitchelli* (A.), *Phascolarctos cinereus* (B.), and *Phalanger orientalis* (C.).

Cl.M: cleido-mastoid; $D.D_1.D_2$: deltoid; H.H: head of humerus; P.M; pectoralis major; S-M: sterno-mastoid; S.D.F: slip of deltoid to forearm: T.R: trapezius.

Phascolarctos it runs to the outer sixth of the clavicle. The attachment is more extensive in *Phascolomys*, for it is fixed to the

outer sixth of the clavicle, the upper border of the acromion, and the spine of the scapula. I believe the extent of this muscle is partly due to varying degrees of functional activity.

Deltoid (text-fig. 39 A–C):—In *Phascolomys* the origin forms a continuous line along the whole length of the clavicle, the acromion and lateral third of the spine of the scapula. The clavicular fibres receive the trapezius, and the acromial fibres and trapezius form a powerful cephalo-humeralis. The clavicular deltoid also fuses with the superficial part of the pectoralis major, and the two are inserted into the pectoral crest. From the scapular fibres a long, narrow, strap-like band runs to the deep fascia over the radial border and dorsum of the forearm and carpus. In *Phascolarctos* the muscle is also entire, the clavicular origin is not so extensive, and the narrow band given off fuses with the supinator longus. In *Phalanger* and *Pseudochirus* the clavicular origin is not as extensive as in *Phascolomys*, the clavicular and acromial parts are separate, and no slip is given off to the forearm.

Scapular Muscles (text-figs. 36–38):—I agree with Macalister (18) that the supraspinatus is larger than the infraspinatus in *Phascolomys* and the Phalangers, but I observed the reverse in *Phascolarctos*. Young (14) states that the infraspinatus is slightly larger than the supraspinatus. The subscapularis and teres major are essentially similar in all, and there is a certain amount of fusion between the latter and the latissimus dorsi and dorso-epitrochlearis. The teres minor is fascial in *Phascolomys*, thin and with a tendinous attachment to the scapula in *Phascolarctos*, and thin and muscular in *Phalanger* and *Pseudochirus*. Even when it is muscular there is a considerable degree of fusion with the infraspinatus. Meckel (6) states that the absence of a teres minor as a distinct muscle appears to be general amongst marsupials.

The characters of the *Coraco-brachialis* in many forms, including the animals described in this paper, have already been recorded, and Cunningham (2) has collected the observations. My own observations do not differ from his.

Biceps:—The two heads of origin are in contact, but not fused, in *Pseudochirus*, and the two bellies (gleno-ulnar and coraco-radial) are fused from the middle of the arm onwards. In the distal portion of the arm the two parts separate again and run to the radial tuberosity and coronoid. In *Phalanger* the tendons of origin are fused to form a tendinous sheet. The muscle bellies remain fused to the distal part of the arm where the stout radial and slender ulnar components are given off. In *Phascolomys* and *Phascolarctos* the origins are conjoined, but the bellies separate sooner from one another in the latter.

Brachialis Anticus:—In all forms it arises on the outer surface of the shaft of the humerus, and winds round it to be inserted into the ulna with, or deep to, the gleno-ulnar component of the biceps. In *Phascolarctos* it is fused with the biceps, but

it is separate from it in *Phascolomys* and the Phalangers. Macalister (18) showed that the conditions in *Phascolomys* are similar to those in many Polyprotodonts and Diprotodonts.

Triceps (text-figs. 36–38):—In *Phascolomys* I observed the long head arising from the lateral two-thirds of the axillary border of the scapula, and the humeral heads are indistinguishably fused. Macalister (8) stated that the long head arises from more than a third of the bone. In *Phascolarctos* the long head arises from a third of the axillary border of the scapula, and it passes to the distal third of the arm before it unites with the fused humeral heads. In *Phalanger* and *Pseudochirus* the long head also arises from a third of the axillary border, but it unites high up with the humeral heads.

Anconei:—The anconeus internus, according to Cunningham (2), is generally present in the Marsupialia. In *Phascolomys*, *Phalanger*, and *Pseudochirus* it is a marked parallel-sided band running from the internal condyle to the olecranon, and the ulnar nerve passes under cover of it. In *Phascolarctos* it appears to be more continuous with the dorso-epitrochlearis. In *Phascolarctos* and *Phascolomys* it is not connected to a fibrous band which gives origin to the flexor carpi ulnaris The anconeus externus is present in all forms, but it is least in *Phascolomys*, in which it has no connection with the triceps.

Pronator Radii Teres:—Cunningham (2) pointed out that this muscle has no coronoid head in the Marsupialia. The insertions vary. In my specimens the conditions are as follows:—

Phascolarctos: to middle two-fourths of the radial shaft.
Phalanger: to distal two-thirds of the radial shaft.
Pseudochirus: to distal two-thirds of the radial shaft.
Phascolomys: to distal half of the radial shaft.

Flexor Carpi Radialis:—This muscle is well developed. It exhibits a variable amount of fusion with the other members of the superficial flexor group, but the fusion is least in *Phascolarctos*. It is inserted into the base of the second metacarpal in *Phascolomys*, *Phalanger*, and *Pseudochirus*, but it runs to the third metacarpal in *Phascolarctos*.

Palmaris Longus is present in all. In *Phascolomys* Macalister (18) described a true palmaris longus and a palmaris accessorius, both arising from the internal condyle. In my specimen the accessorius does not arise from the condyle, but it is implanted into the side of the tendon of palmaris longus in the distal third of the forearm; and it has a very slender tendon which runs to the palmar pad. In *Phascolarctos*, *Phalanger*, and *Pseudochirus* there is no trace of the accessorius.

Flexor Carpi Ulnaris:—In all the animals described in the present paper the insertion is into the pisiform bone. But Macalister (18) described it as being attached to the fifth metacarpal in *Phascolomys*. Young (14) describes it as giving off

prolongations to the fifth metacarpal and the unciform in *Phascolarctos*.

Flexor Sublimis Digitorum:—This muscle is frequently strongly connected to the flexor profundus, and it is sometimes called the flexor perforatus because the profundus tendons pierce its tendons, which are very slender. The sublimis and profundus tendons separate out from the strong flexor mass in the distal part of the forearm.

Pronator Quadratus:—The extent of the interosseous space occupied by the pronator quadratus varies considerably. In *Phascolomys* I observed it extending over the distal half of the space, but Macalister says it is weak and only occupies the distal third. In *Phascolarctos* it occupies the lower fifth, but the extent is even less in *Phalanger* and *Pseudochirus*. Cunningham (2), however, described it as covering one third of the bones in Cuscus (*Phalangista maculata*).

Supinator Longus:—My observations on *Phascolarctos* differ in some respects from those of Macalister (5) and Young (14). It consists of two parts. The proximal division arises from the shaft of the humerus from close to the neck downwards, and it is thin and almost aponeurotic. The distal part, which is more muscular, arises from the lateral supracondylar ridge and by fibres which fuse with the extensors of the wrist. The two parts unite into a strong tendon which, passing under the abductor pollicis major, is inserted into the scapho-lunar bone. Young points out that it is both a radial flexor and supinator. It receives a slip from the deltoid. In *Phalanger* it is also large, but not divided into two parts. It springs from the proximal two-thirds of the lateral supracondylar ridge. No slip runs into it from the deltoid. These conditions are also present in *Pseudochirus*. The conditions in *Phascolomys* are, however, very different. It is thin and aponeurotic in parts, and it receives a strong band from the deltoid.

Supinator Brevis:—The extent of the radius embraced by this muscle varies. In *Phalanger* it covers less than the upper fifth, in *Phascolarctos* it covers the upper fifth, and in *Phascolomys* it envelops the upper two-thirds.

Extensores Carpi Radiales:—The existing records show that there is considerable variation in these muscles in the Marsupialia. In *Phascolomys* there is a single muscle arising from the external condyle and lateral ridge of the humerus and running to be inserted into the second and third metacarpal bones. But it is evident that the long and short extensors are combined in the single muscle. In *Phascolarctos* both long and short extensors are present and are inserted into the radial borders of the second and third metacarpals respectively. In *Phalanger* both muscles are present, but the brevior is a large and powerful muscle with three heads of origin as described by Cunningham (2).

Extensor Communis Digitorum:—In all forms it arises from the external condyle. In most Marsupialia it sends four tendons

to the four inner digits. But, as Young (14) mentions, and I observed myself, tendons go to each of the five digits in *Phascolarctos*.

Extensor Secundus Digitorum :—This muscle, which corresponds to the extensor minimi digiti of human anatomy, has been fully described in many Marsupialia by Cunningham (2), Young (14), and Macalister (5 & 18). In *Phascolarctos* it is in reality double. One muscle runs to the third digit as an extensor medius, and the other is inserted into the fourth and fifth digits. In *Phascolomys* and the Phalangers only the latter part is present.

Extensor Carpi Ulnaris:—In *Phascolomys* it arises from the external condyle of the humerus and upper part of the shaft of the ulna, and is inserted into the mesial border of the shaft of the fifth metacarpal bone. In *Phascolarctos* the ulnar origin head is similar to the above. But in *Phalanger* there is no ulnar head.

When a superficial view of the extensor muscles is taken in all the animals described in this paper, it is seen that intermuscular septa are well marked in *Phascolarctos*. In *Phascolomys* and the Phalangers there is more fusion of the bellies of the muscles.

Extensor Ossis Metacarpi Pollicis:—This muscle, as has already been pointed out by several authors, includes the extensor primi internodii pollicis. In *Phascolomys*, according to Macalister (18), it arises from the dorsum of the shaft of the ulna and the interosseous membrane, crosses the extensor carpi radialis tendon, and is inserted into the trapezium and thumb metacarpal. In *Phascolarctos* I observed it arising from the dorsum of the proximal third of the part of the ulna bordering the interosseous space, from the membrane, and from the greater part of the dorsum of the radius from the orbicular ligament distally. In *Phalanger* and *Pseudochirus* it also arises from both bones and the interosseous membrane, but the ulnar origin is lower and more extensive than in *Phascolarctos*, and the muscle belly gives off two tendons which wind over the extensor carpi radialis and supinator longus tendons.

Extensor Secundi Internodii Pollicis:—There is no trace of this muscle in *Phascolarctos*, and in this respect I agree with Young (14) and differ from Macalister (5), who stated that it is arranged as usual. In *Phascolomys* it runs from the lower third of the ulna to the last phalanx of the pollex. The tendon gave a short slip to the fascia over the metacarpo-phalangeal joint of the index. In *Phalanger* it also gives slips to the index and pollex, and Cunningham (2) describes two separate muscles in *Phalangista maculata*. It is therefore evident that the only extensor of the pollex in *Phascolarctos* is the additional tendon of the extensor communis digitorum ; and in no other Marsupial is this arrangement present.

Intrinsic Muscles of the Manus:—The observations of Cunningham (2), Macalister (5, 18), Ruge and Young (14, 15) have given us a very complete account of the anatomy of these muscles. Young, in particular, has shown how they have become

modified in accordance with habits. He has also shown that the Koala is very different from the others, his conclusions being as follows:—"The digits form two groups, of which one, including the thumb and index finger, is opposable to the other, this latter comprising the three remaining digits. The index digit, in point of fact, constitutes a second thumb; and, in comformity with its unusual freedom of action, its special muscles are well developed. Moreover, as the result of the arrangement of the digits into two groups, the middle line of the hand no longer passes through the *third* digit, but along the *fourth*. The muscles of the hand are correspondingly modified, and hence, so far as regards their insertions, the arrangement is very different to what is ordinarily found."

Muscles of the Posterior Extremities.

Gluteus Maximus:—In *Phascolarctos* it has no origin from the iliac crest, but springs from the sacral and caudal vertebræ. The coarse fibres sweep over the great trochanter, thereby producing a rounded prominence, and are inserted into a considerable length of the femoral shaft. The fibres are continuous postero-mesially with the *lateralis caudæ*. In *Phascolomys* a broad, long agitator caudæ shuts off the gluteus maximus from the sacral and caudal vertebral spines, and a strong intermuscular septum, which gives origin to some of the fibres of both muscles, intervenes between them. The gluteus maximus also arises, as in all Marsupialia except the Koala, from the iliac crests posteriorly, and from the lumbar fascia. The whole muscle appears flattened, and it is inserted into the back part of the great trochanter. Cunningham (2) describes how the gluteus maximus is divided into three parts in *Phalangista maculata*, but there is no obvious separation into distinct parts in my specimen of *Phalanger orientalis*. There it is a long fan-shaped sheet composed of gluteus maximus, tensor fasciæ femoris, and agitator caudæ. It extends from the lumbar fascia anteriorly backwards along the iliac crest and spines of the sacral and anterior four caudal vertebræ. The part of the sheet representing the agitator caudæ has much coarser fibres than the other parts. The insertion of the sheet does not differ in any essential point from that in *Phalangista maculata*, already described by Cunningham. In *Pseudochirus* the conditions resemble those in *Phalanger*, but the fibres of the agitator caudæ are not so coarse, or so separate from the other parts of the muscle.

Gluteus Medius:—In all forms it is large, and frequently exceeds the maximus in size. In *Phascolarctos* it arises from the iliac crest, the gluteal surface of the ilium, and the sacral spines. It is inserted into the great trochanter. The fibres are in parts fused with the subjacent gluteus minimus, but there is no lamination as described by Young (14). In *Phascolomys* it is difficult to separate the medius and mimimus. In *Phalanger* and *Pseudochirus* the medius and minimus are separate. The *Gluteus*

Minimus does not differ in any essential in the animals described in this paper except for the degree of adhesion to the medius. The *Gluteus Quartus* is present in all.

Pyriformis:—In all forms this is a strong triangular muscle arising from the side of the sacrum and running to the summit of the great trochanter of the femur. The *Obturator Externus* is likewise similar in all, and is large.

Obturator Internus:—This muscle is absent in *Phascolomys*, but present in all other forms. The *Gemelli* are present in all. They are both enormous in *Phalanger*, of moderate size in *Phascolarctos*, and the inferior one is large in *Phascolomys*.

The *Quadratus Femoris* is absent in *Phascolomys*. In *Phascolarctos* it arises entirely from the great sciatic ligament. In *Phalanger* it arises from the tuber ischii. The insertion is into the posterior border of the great trochanter.

Sartorius:—In the Marsupialia this muscle acts as an extensor, and an interval, filled with fascia, is present between its upper part and the quadriceps. It arises in all from the anterior superior iliac spine; and it is inserted into the inner side of the quadriceps tendon (*Phascolarctos*), or the inner aspect of the patella and knee-joint (*Phalanger*, *Pseudochirus*, *Phascolomys*).

Quadriceps Extensor:—The rectus femoris has only the straight head in *Phascolomys*, but both heads are present in *Phascolarctos*, *Pseudochirus*, and *Phalanger*. In the other elements these animals are all essentially similar, and the vastus externus component is large. The tendon is inserted in all into the tibia. It contains a cartilaginous patella in *Phascolomys*, *Phalanger*, and *Pseudochirus*, but none in *Phascolarctos*. Waterhouse (**17**) stated that *Phascolomys* also has no patella, and used this character among others to show that they are related. As many observers have recorded the presence of the patella in the Wombat, it is evident that this is not a character linking it to the Koala, as Waterhouse believed.

Gracilis:—When the skin is removed it is seen that the muscles on the mesial aspect of the thigh are concealed by the gracilis to a variable extent. It arises from the symphysis pubis and a variable extent of the descending ramus, and from the mesial extremity of the marsupial bone. It is inserted into the proximal half of the mesial border of the shaft of the tibia. In *Phascolomys*, *Phalanger*, and *Pseudochirus* it goes to the proximal half of the tibia, but in *Phascolarctos* it only runs to the proximal third.

Biceps Cruris:—In *Phascolarctos* the biceps and semimembranosus have a strong, common tendon of origin from the ischial tuberosity and caudal vertebræ. The biceps is thin and triangular, and inserted into the fascia over the proximal two-thirds of the fibula. No femoral component enters into the biceps. Young (**14**) points out that the nature and extent of the insertion are associated with the semi-flexed attitude of the limb. In *Phalanger* the muscle arises from the ischial tuberosity, along with semi-

membranosus, and from the caudal vertebræ, the two parts being separate. No femoral head is present. The ischial part expands and becomes fan-shaped; it is inserted into the fascia over the fibula in the proximal two-thirds of the leg. The caudal part is at first superficial to the ischial part, but winds round it and divides into two portions. One of these fuses with the ischial part. The other fuses with semitendinosus, and then is inserted into the middle of the subcutaneous mesial surface of the tibia. The conditions present differ in several respects from Cunningham's account of the muscle in *Phalangista maculata*. In *Pseudochirus* the conditions are essentially similar to those in *Phalanger*. In *Phascolomys* it arises entirely from the ischial tuberosity along with semimembranosus, and it is inserted into the fascia over the proximal third of the fibula, and into the bone itself, but it is not divisible into two parts as in the Phalangeridæ. No femoral head is present. Its insertion is less than in *Phascolarctos* and the Phalangeridæ.

No bicipiti accessorius is present in any of these animals.

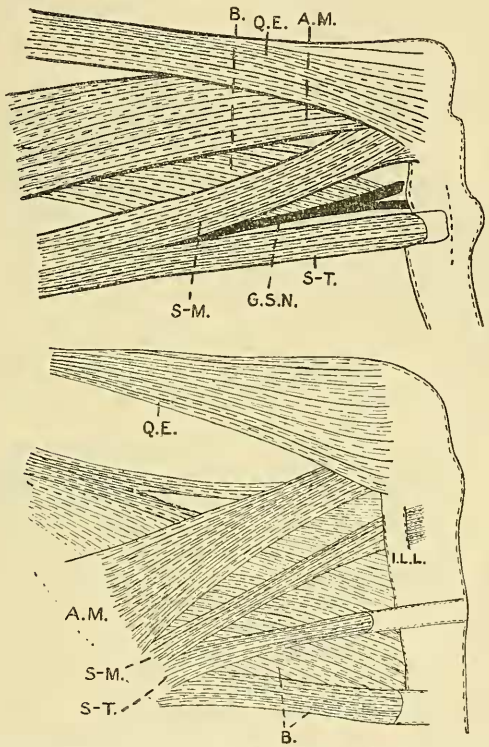
Semimembranosus (text-fig. 40):—In all forms it is muscular from origin to insertion, and there is a variable amount of union to the biceps; and the course in all is from the tuber ischii to the mesial aspect of the leg. In *Phascolarctos* it is inserted into the quadriceps tendon, internal tuberosity of the tibia, and the fascia of the leg; and some of the fibres fuse with the triceps adductor femoris. In *Phalanger* the insertion is moved farther distally. It avoids the adductor and quadriceps, passes under the internal lateral ligament of the knee, and is attached to the anterior tuberosity of the tibia. And, as Cunningham (2) pointed out in *Phalangista maculata*, it must rotate the leg on the thigh and act as a powerful flexor. In *Phascolomys* it is inserted into the mesial aspect of the head of the tibia.

Semitendinosus (text-fig. 40):—In *Phalanger* it is inserted into a narrow strip of the middle of the ventral border of the shaft of the tibia. But Cunningham (2) described it as going to the mesial surface of the bone in *Phalangista maculata*. In *Phascolarctos* it is inserted into the mesial aspect of the tibia at the level of the prominent tubercle on the anterior (ventral) border. In *Phascolomys* it runs to the mesial border of the tibia in its middle third. No tendinous inscription is present in any of these Marsupialia. The muscle fuses with the biceps in *Phalanger* and *Phascolomys*, but is quite free in *Phascolarctos*. But Macalister (18) described it as free from other muscles in *Phascolomys* and *Phalanger*.

Gastrocnemius:—In *Phalanger*, as in *Phalangista maculata*, the two parts from origin to insertion are quite separate. The inner head arises from the back of the internal condyle of the femur, and its tendon is inserted into the tuberosity of the os calcis. The outer head arises from the proximal sixth of the shaft of the fibula and from the intermuscular membrane between it and the peronei; its tendon is inserted into the tuberosity of the

os calcis deep to that of the mesial part of the muscle. Only a thin membrane connects the two parts. In *Phascolarctos* the two parts arise as in *Phalanger*; at the junction of the proximal and middle thirds of the leg a strong, narrow aponeurosis, which ultimately forms the tendo Achillis, begins to appear on the outer part of the muscle, and the inner part is attached to it. In

Text-figure 40.



Adductor and hamstring muscles of *Phascolarctos cinereus* (above), and *Phalanger orientalis* (below).

A.M: adductors; B: biceps; G.S.N: great sciatic nerve; I.L.L: internal lateral ligament of knee; Q.E: quadriceps extensor; S-M: semi-membranosus; S-T: semi-tendinosus.

Pseudochirus the two parts unite, so it resembles that in *Phascolarctos* rather than *Phalanger*. In *Phascolomys* the inner head arises from the back of the internal condyle, and from a small piece of the popliteal surface of the femur on both mesial and lateral aspects. The outer head arises from the sesamoid bone at the back of the external condyle. Both remain separate for a considerable distance, the mesial part overlapping the lateral one,

But they are inserted into a tendo Achillis. It is therefore evident that the degree of separation of the internus and externus differs in these Marsupialia.

Soleus:—In *Phascolarctos* and *Phalanger* there is no separate soleus, and the observations of Cunningham (2), Macalister (5), and Young (14) have shown that it is really contained within the gastrocnemius externus, as the latter has a fibular origin. Moreover, the plantaris lies under cover of the inner part of gastrocnemius externus, and not under the part which corresponds to soleus. In *Phascolomys* the soleus has a small fibular head, but no tibial origin.

Plantaris:—In *Phalanger* and *Phascolarctos* it is well developed, and it is inserted into the plantar fascia, but Young (14) observed it inserting into the tendo Achillis in one Koala. In *Phascolomys* it is absent.

Tibialis Anticus:—In all forms it arises from the outer surface of the shaft of the tibia, and the interosseous membrane; but its insertion varies. In *Phascolomys*, according to Macalister (18), it is inserted into the entocuneiform. In my specimen two tendons are given off. One goes to the entocuneiform, and the other to the hallux. The latter takes the place of the extensor longus hallucis, which is absent as a separate muscle in my specimen. In *Phalanger* and *Phascolarctos* the insertion is into the entocuneiform alone. And in these genera a separate extensor hallucis arises from the fibula.

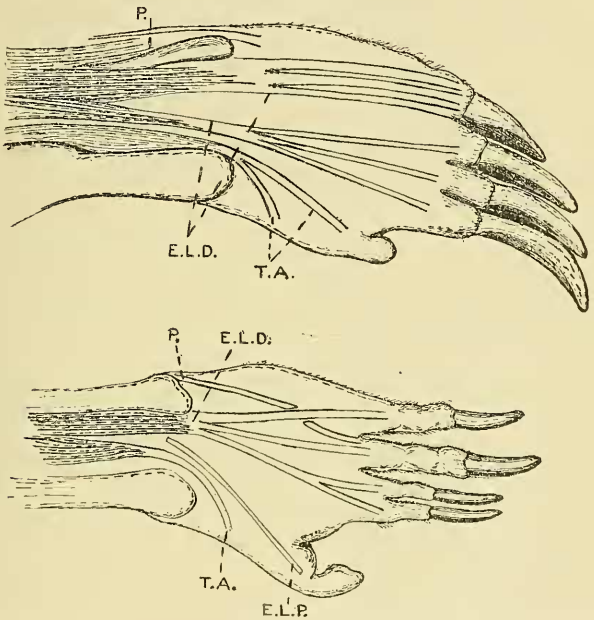
Extensor Digitorum Longus:—Macalister (18) describes it in *Phascolomys* as arising from the fibula and front of the tibia, and running to the four toes. In my specimen (text-fig. 41) it arises from the tibia, fibula, and interosseous membrane. It soon divides into slender inner and stout outer portions. The former gives three delicate tendons to the first, second, and third toes, but the three stout tendons of the lateral portion go to the inner, dorsal, and lateral parts of the inner toe. In *Phascolarctos* (text-fig. 41) the muscle likewise consists of two parts, whereas Young (14) states that in being separable into two portions the Koala differs from such marsupials as have been examined. Three tendons emerge. The first is slender and divides into slips for index and medius. The second is of medium size and runs to annularis. The third is powerful and divides into tendons to annularis and minimus. In *Phalanger* three tendons are disposed as in *Phascolarctos*, but the muscle itself is not divisible into two. There is, therefore, a greater resemblance between these arboreal forms than there is between *Phascolarctos* and *Phascolomys*.

Peronei:—The muscles composing the groups differ considerably. In *Phascolarctos*, as pointed out by Young (14), there are four components—longus, brevis, quarti metatarsi, and quinti metatarsi,—and all are fibular in origin. In *Phalanger*, as in *Phalangista maculata*, there are three components—longus, brevis, and some muscular slips representing portions of the extensor brevis digitorum. In *Phascolomys* Macalister (18) described long and

short peronei and an accessory quinti tendon detached from the last for the first phalanx of the outer toe. In my specimen this last slip is absent, but I believe it is represented by one of the slips of the extensor longus digitorum.

Ruge pointed out that the *extensor brevis digitorum* was originally derived from the peroneal group of muscles. It is present in all Marsupialia, but varies in the degree of development. In *Phalanger* it runs to the four toes. In *Phascolarctos* it is

Text-figure 41.



Extensors of foot in *Phascolomys mitchelli* (above) and *Phascolarctos cinereus* (below).

E.L.D: extensor longus digitorum; E.L.P: extensor longus hallucis; P: peronei; T.A: tibialis anticus.

inserted into the two inner toes. And in both forms it arises from the fibula. In *Phascolomys* it arises fron the outer part of the tarsus, and is inserted into the inner pair of toes.

Tibialis Posticus:—This muscle has already been fully described by Cunningham (2), Young (14), and Macalister (5, 18). In *Phascolomys* it is a single muscle arising from the back of the tibia and running to the inner part of the scaphoid. In *Phascolarctos*, *Phalanger*, and *Pseudochirus* it is double. In the Koala two fibular slips run to the scaphoid and entocuneiform; but in the Phalangers both tibial and fibular bellies run to the scaphoid.

The *flexor longus digitorum* includes flexor longus hallucis, and arises from tibia and fibula. Superficial and deep tendons are present, and the latter pierce the former, as in the manus.

The *popliteus* occupies practically the whole interosseous space.

The intrinsic muscles of the pes have already been fully described (2), and the mid line in *Phascolarctos* has been moved, as in the case of the manus, with resulting modifications in structure.

Summary of Myological Features.

1. In all animals described in this paper there are traces of adherence to the primitive lamination which characterises the development of mammalian muscles in general. In *Phalanger*, *Pseudochirus*, and *Phascolomys* we observe:—1. Inseparability of the prevertebral muscles; 2. Undivided state of the rhomboideus; 3. Fusion of the trapezius with the pectoral fascia and clavicular deltoid; 4. Biceps flexor cruris has only one head of origin; 5. Separate character of the hamstrings; 6. Degrees of separation of levator scapulæ and serratus magnus. In *Phascolarctos* the following additional ones are present:—7. Platysma continuous with muscles of orbit, auricle, and mouth; 8. Sterno-hyoid prolonged to mandible; 9. Styloid muscles a single sheet; 10. Digastric and mylo-hyoid fused; 11. Hyoglossus transverse and not attached to hyoid; 12. Omo-hyoid passes into tongue; 13. Internal oblique has tendinous intersections; 14. Quadratus lumborum absent; 15. Supinator longus very long; 16. Pronator quadratus small; 17. Coraco-brachialis double; 18. No extensor secundi internodii pollicis; 19. Origin of gluteus maximus; 20. No soleus; 21. Tibialis posticus double; 22. Characters of peronei; 23. Intrinsic muscles of manus and pes.

2. Many of the myological features are similar in all these animals, in many other Marsupials, and in animals belonging to the other Mammalian orders.

3. Most of the characters not included in the above groups are adaptations to suit modes of life.

4. In the small group of characters—omo-trachelian and deltoid—not included in the three preceding groups, the Koala and Wombat differ from the Phalangers.

Classification.

All zoologists have separated *Phascolomys* from the Phalangeridæ, so the work of the systematist is limited to fixing the proper position for *Phascolarctos*. To do so it is necessary to examine all characters, both external and internal. The large assemblage of data so obtained must then be reduced by excluding characters of little or no value for purposes of classification. In the first place, one must remove those which are varying degrees of persistence of primitive conditions which were once present in their common ancestor. Secondly, structures which are similar as

the result of convergence must be excluded as they are not evidence of affinity. Thirdly, those features which are common to all the animals under consideration, to many other Marsupials, and to other Mammals cannot be employed in making a classification of the Wombat, Koala, and Phalangers. We are then left with a series of useful characters, and those which are sheltered deep down in the body should be of value, for they are less liable to be influenced by climate and habits than are the more superficial characters.

The anatomical characters must be arranged in four groups :—

A. Those in which *Phascolarctos* and *Phascolomys* differ from the Phalangeridæ. They support the systems of Weber (12) and Winge (13), and Weber's family of Phascolarctidæ is employed here for the Koala and Wombat.

B. Those in which *Phascolarctos* and the Phalangeridæ differ from *Phascolomys*. Special attention must also be paid to the comparison between *Phascolarctos* and *Pseudochirus*. These support the systems of Thomas (11), Bensley (1), and Gregory (4).

C. Characters in which *Phascolarctos* differs from *Phascolomys* and the Phalangeridæ.

D. Characters differing in all forms.

Groups C and D are evidence in favour of Pocock's system.

In estimating the value of the anatomical data one must always bear in mind the habits and the character of the diet of these animals. *Phascolarctos* and the Phalangeridæ are arboreal animals, but lead different kinds of life. The latter are active, but the former is a clumsy, sluggish creature, clinging to branches by its modified feet. *Phascolomys*, on the other hand, is an active animal. Its hind-limbs are fossorial and its fore-limbs are for active progression. A study of the myology shows that these modes of life are accompanied by numerous differences in the muscles. As regards the diet, that of *Phascolarctos* and *Phascolomys* is bulky, whereas that of the Phalangeridæ is not ; and the Phascolarctidæ have specialisations in the structure of their alimentary canal to meet the demands imposed by it. Finally, although the life habits differ, we find the arboreal sluggish Koala and the active fossorial Wombat possess numerous characters of great importance in their skeletons and soft parts, in which they differ from the active arboreal Phalangeridæ. We must always aim at discovering the part played by each structure in the animal economy before we can assess its true systematic value. Some characters are well understood, but there are others of whose general adaptive purpose we are totally ignorant.

A. *Characters in which the Phascolarctidæ differ from the Phalangeridæ.*

External Characters :—Pocock (9) showed that the supratragus in the Phalangers and many other Mammals is a prominent ridge with a well-developed lobe ; but it is low, inconspicuous, and

devoid of lobate thickening in the Phascolarctidæ. This, in my opinion, is a character of importance, for it does not appear to depend on modes of life. Pocock has also shown how the various genera can be separated by the auricular characters. As regards the mammæ the Phascolarctidæ have only two, but the Phalangeridæ have four. Pocock found two only in *Trichosurus*. The tail is a well-developed organ in the Phalangeridæ, and rudimentary but muscular in the Phascolarctidæ; probably the reduction is the result of life habits. The Koala clings only by its hands and feet to the branches, so the tail would be useless; and a tail would be in reality an impediment to the Wombat. The Phalangeridæ have vibrissæ on the wrist and hind foot, but no traces of these tactile hairs are present in the Phascolarctidæ. Moreover, the integuments of the hind feet differ. In the Phalangeridæ the skin is striated over the well-marked pads, but it is granular on the reduced pads in the Phascolarctidæ.

Myology:—In the Phascolarctidæ there is no cleido-occipital, the omo-trachelian is single, and the unbroken deltoid gives a slip to the forearm. In the Phalangeridæ, on the other hand, the cleido-occipital is present, the omo-trachelian is double, and the deltoid, which is in two parts, does not give a slip to the forearm. Although these are prominent differences, they are of very minor importance in classification.

Circulatory System:—In the Phascolarctidæ the pericardium adheres to the diaphragm, the post-caval vein does not conceal the abdominal aorta, and anterior jugular veins are absent. In the Phalangeridæ the pericardium is connected to the diaphragm by two membranous sheets, and the post-caval vein conceals the posterior part of the abdominal aorta. I found anterior jugular veins in *Trichosurus* and *Phalanger*, but not in *Pseudochirus*; perhaps they exist in the latter, for my specimens had been preserved so long in spirit that the veins, if present, had shrunk to minute proportions.

Alimentary Canal:—Cheek-pouches are absent in the Phalangeridæ, but present in the Phascolarctidæ; they are well-marked in *Phascolarctos*, but rudimentary in *Phascolomys*. I believe, however, that these diverticula are, in reality, adaptive in function. The stomach is simple in both families, but possesses the so-called gastric gland in the Phascolarctidæ. That structure has been regarded by many zoologists as of special value for showing the close relationship between *Phascolarctos* and *Phascolomys*. Indeed, Forbes (3) regarded it as the main test. But Johnstone (16) showed that it is no special gland; it is an evagination and folding of the mucous membrane plus an extension of the normal gastric glands. It is in reality a means of increasing the secreting area of the stomach to fulfil the demands imposed by a bulky diet. The Phalangers do not consume a bulky diet, so cheek-pouches are absent, and there is no trace of the gland patch. Unless there were other characters showing a close relationship between

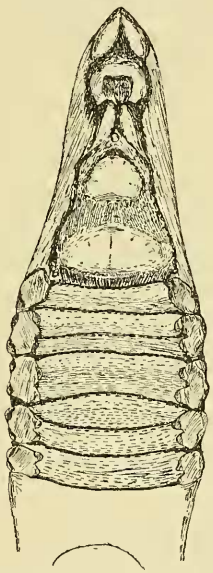
Phascolarctos and *Phascolomys* the gland patch alone could not be employed as a test of affinity.

The liver also possesses distinguishing characters. In the Phalangeridæ the caudate lobe is present, but the main lobes are not complicated by secondary sulci. In the Phascolarctidæ, on the other hand, there is no caudate lobe, and many secondary sulci subdivide the main lobes.

Phascolarctos predominates over *Phascolomys* in the size of the cheek-pouches, the complexity of the gland patch, the subdivision of the main hepatic lobes, and the length of the gall-bladder.

As regards the dentition, Waterhouse (**17**) pointed out long ago

Text-figure 42.



The hard palate in *Phascolomys mitchelli*.*

that "the approximation to the Rodent-like dentition which is exhibited by the Wombat is perceptible in the Koala, in the smaller development of the posterior incisors and canines of the upper jaw, and the total absence of those premolars which, in the typical Phalangers, intervene between the canine and the five molars of the upper jaw, and the incisor and corresponding teeth in the lower jaw." Bensley (**1**) has shown, however, that the dental characters which would point to a resemblance between *Phascolarctos* and *Phascolomys* are probably due to convergent evolution, and Forbes (**3**) rightly considered that the dental characters in *Phascolomys* are adaptive in

* Compare with Plate V in my paper on the Koala (**10**).

character. Tomes (19) showed that the dental enamel in *Phascolomys* possesses histological characters which separate it from most, if not all Marsupialia, but he did not specifically mention *Phascolarctos*. It appears, therefore, that in the dentition we have an assemblage of characters brought about by adaptation and convergence, so they cannot be used to show a close affinity between the Koala and Wombat.

Generative Organs and Development:—In the Phascolarctidæ the vaginal culs-de-sac are separate, but they coalesce in some of the Phalangeridæ, at least in *Trichosurus* (Forbes). As regards the fœtal membranes, Professor J. P. Hill informs me that they are fundamentally the same, but differing in details, in the Koala and Wombat. Moreover, the conditions in the Phascolarctidæ differ entirely from those in the Phalangeridæ.

Osteology:—I have compared the conditions in the material at my disposal with Owen's account (8), and the essential points are shown in the subjoined table:—

Phascolarctidæ.	Phalangeridæ.
1. Pterygoid processes large.	1. Processes small.
2. Intermaxillary bones increased transversely.	2. Bones not increased transversely.
3. Palatal process of maxilla forms a considerable part of boundary of incisive foramina.	3. Maxillæ form a small part of boundary.
4. Palatal foramina entirely on palate bones.	4. Palatal foramina extend into maxillæ.
5. Groove obsolete.	5. Groove runs from foramen rotundum to Gasserian fissure.
6. Not ossified.	6. Margin of tentorium ossified.
7. Mid spongy bone simple *.	7. Convolutions of mid spongy bone numerous and delicate.
8. Halves of mandible united.	8. Halves separate.
9. Seventh cervical vertebra perforated.	9. Not perforated.
10. Process beneath the sixth cervical process short.	10. Process greatly expanded.
11. Anterior arch of the atlas partly cartilaginous.	11. Arch entirely osseous.

In many of the osteological characters not included in the above list there are differences in degree only in the Phalangers, *Phascolarctos*, and *Phascolomys*. Doran has shown that the ear ossicles of *Phascolarctos* differ entirely from those in the Phalangeridæ, but they have some points in common with those of *Phascolomys*.

B. *Characters in which Phascolarctos and the Phalangeridæ differ from Phascolomys.*

External Characters:—In *Phascolomys* flaps of skin from the lower lip protrude into the diastemata, but this is a new development, associated, as in many Rodentia, with the type of dentition. There is, however, no trace of these in the other animals. As

* Owen's account is relied on here as the skulls in my possession are not perfect as regards the turbinate bones.

regards the manus and pes, it is necessary to consider both the external appearances and the internal structure. Pocock (9) and others have already described the external appearances, and the following conclusions can be drawn from their accounts:—

1. The fore foot possesses no special modifications in *Trichosurus*.

2. The conditions in *Phascolomys*, which are adapted for a fossorial and ambulant life, have some resemblance to those of *Trichosurus*, but differ in many ways from those in *Phascolarctos* and the Phalangeridæ. Among these are the length of the digits, the shortness and bluntness of the claws; and there is no division of the digits into two opposing groups. The pads are reduced.

3. In *Phascolarctos* and the Phalangeridæ the pollex and index can be opposed to the long axis of the manus, and Young regarded these two digits as constituting one group, the remaining three digits forming a second. These conditions are slightest in *Phalanger*, intermediate in *Pseudochirus*, and most highly developed in *Phascolarctos*. The latter differs from all Phalangers, except *Trichosurus*, in the appearance of the pads. In *Phalanger* and *Pseudochirus* the pads are striated, but they are granular in *Phascolarctos* and *Phascolomys*. Moreover, myological literature shows that *Phascolarctos* is peculiar in many ways. I agree with Pocock's scheme, which shows that the characters of the manus in *Phascolomys* differ from those in the other animals. And although the others have features in common, there are sufficient characters to distinguish *Phascolarctos* from the Phalangeridæ.

Bensley (1) described and figured the pes of the Diprotodonts, and drew important conclusions as regards the affinities of the animals. He pointed out that the pes in *Dromicia* is prototypal for the Phalangeridæ, and those of *Phalanger* and *Pseudochirus* conform more or less closely to it. But the conditions in *Phascolarctos* show no close relation to those in *Pseudochirus*. The general conformation of the digits is the same, but the pads are all reduced, the sole being covered with soft, granular skin as in *Phascolomys*. The hallux is much farther back than in *Pseudochirus*, so it is more perfectly opposable. A slightly greater displacement would put its axis in line with that of the fourth digit, which it opposes. The foot differs in *Phascolarctos* and *Phascolomys* both in external appearance and internal structure.

Although the pes of *Phascolarctos* differs from that in *Pseudochirus* the dental characters are similar, but reach a higher degree of development in the former. Bensley (1) showed that these genera have quadrituberculate molars with selenoid cusps. The upper teeth have reduced external styles, with or without intermediate conules. In *Phalanger* and *Trichosurus* the quadrituberculate molars have bunoid cusps. And the upper teeth have neither external styles nor intermediate cusps. Moreover, as

shown on page 889, there are some resemblances between the teeth of *Phascolarctos* and *Phascolomys* which have resulted from convergence. These, however, must be excluded for purpose of classification.

Osteology :—The contrast in the skeletal characters are tabulated as follows :—

Phascolarctos and the Phalangeridæ.	*Phascolomys*.
1. Zygoma extended vertically and has no twist.	1. Zygoma has a marked twist.
2. Elements of occipital bone confluent.	2. Elements not all confluent in many skulls, but not in all.
3. Characters of supra-occipital.	
4. Occipital processes arise from ex-occipital.	4. Processes from petro-mastoid.
5. Bulla from alisphenoid.	5. Bulla from temporal bone.
6. Petrous has a large cerebellar pit.	6. Pit obsolete.
7. Six pieces in sternum.	7. Four pieces in sternum.
8. Characters of humerus.	
9. No third trochanter on femur.	9. Third trochanter present.

Myology :—*Phascolomys* differs from the Phalangeridæ and *Phascolarctos* in the absence of the quadratus femoris, obturator internus and popliteus, and in having only one head to the rectus femoris.

Circulatory System :—*Phascolomys* has no trace of a vena transversa (text-fig. 32).

It is necessary to remark on the comparison between *Phascolarctos* and *Pseudochirus*, because these have been placed close together in systems of classification. In a detailed examination of their anatomy one finds they differ from other Phalangers and *Phascolomys* in the character of the teeth and straightening out of the inflected angles of the mandible. As regards the visceral anatomy and myology, there is no way in which they can be marked out from other forms. I can see no reason other than the condition of the teeth and mandible for separating *Pseudochirus* from the other Phalangers, but I consider these alone as sufficiently important to do so.

When the characters mentioned in groups A and B are reduced by the elimination of the unimportant ones the following lists are obtained :—

A. Characters separating the Phascolarctidæ from the Phalangeridæ :—

1. Supratragus, tarsal vibrissæ, skin of pads and tail.
2. Gastric gland patch and liver.
3. Fœtal membranes.
4. Position of palatal foramina.
5. Characters of symphysis menti.
6. Characters of the mid-turbinal bone (Owen).
7. Characters of the ear ossicles.

B. Characters separating *Phascolomys* from *Phascolarctos* and the Phalangeridæ :—

1. Formation of the alisphenoid bulla.
2. Site of occipital processes.
3. Pieces in sternum.
4. Third trochanter of femur.
5. Dentition.
6. Some of the characters of manus and pes.

C. *Characters in which Phascolarctos differs from the Phalangers and Phascolomys.*

External Characters :—Pocock (9) showed that there is a rhinarium in *Phascolomys* and the Phalangeridæ, but no true rhinarium is present in *Phascolarctos*; and the nostrils of the latter are also peculiar. In the same paper he deals with the characters of the marsupium, and points out that *Phascolomys* is intermediate between the Phalangeridæ and *Phascolarctos*. Moreover, the pouch of the latter is not closely related to that of any genus of the Phalangeridæ.

Myology :—In the summary of myological features at the end of the first part of this paper I enumerated many conditions representing adherence to the primitive lamination of the muscles. But these cannot be used for purposes of classification.

The other points are given in the following table :—

Phascolarctos.	*Phascolomys* and Phalangeridæ.
1. Occipital crest curves backwards.	1. Not so.
2. Alisphenoid bullæ as long as ex-occipital processes.	2. Not so in Phalangers. Bulla temporal in *Phascolomys*.
3. Characters of nasal bones.	
4. Anterior margin of septum nasi concave.	4. Convex.
5. First dorsal spine scarcely exceeds seventh cervical.	
6. No patella.	6. Patella thin and cartilaginous.
7. Vagina musculina present.	7. Absent.
8. No azygos lobe.	8. Right lung has azygos lobe.
9. Epiglottis entire and far from tongue.	9. Epiglottis notched and close to tongue.
10. No faucial tonsil.	10. Faucial tonsils present.
11. Thick ureteric venous plexus.	11. Absent.

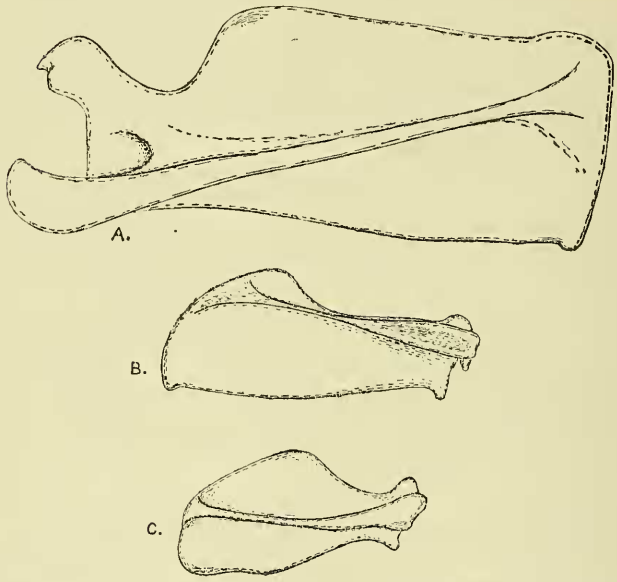
D. *Characters differing in all forms.*

In the first part of this paper I described no fewer than thirty-two myological features differing in all forms. But these fall into primitive and adaptive groups, and are useless for purposes of classification. As regards visceral anatomy, there are many points differing in all forms. Some of these are undoubtedly

adaptive, but others cannot be included in that category. The visceral and osteological characters are tabulated as follows:—

1. Oral vestibule, palatal formula, tongue.
2. Spleen, thymus, cervical lymph-glands.
3. Division of the right auricular appendix.
4. Branches of the aortic arch.
5. Number of dorsal vertebræ, ribs, intercostal soft parts.
6. Relative length of facial part of skull.
7. Characters of glenoid cavity.
8. Size and perforations of lachrymal bone.
9. Characters of scapula.

Text-figure 43.



The scapula in *Phascolomys mitchelli* (A.); *Phascolarctos cinereus* (B.); and *Phalanger orientalis* (C.).

Conclusions.

From an examination of these four groups of characters I have come to the following conclusion:—

1. *Phascolarctos* cannot be included in the Phalangeridæ. Although dentition and foot structure have led some observers to put it in that family in close relation to *Pseudochirus*, there are many very important points in which it differs from them. If they are united it will be by superficial characters, and one will

break up the series of fundamental characters uniting the Koala and Wombat.

2. *Phascolarctos* is united to *Phascolomys* by characters whose importance far outweighs the resemblances between the former and the Phalangeridæ. The major ones enumerated on page 892 are regarded as of value by anatomists and evolutionists.

3. The characters peculiar to *Phascolarctos* are not sufficiently important to place it in a separate family. But they are useful for distinguishing it from *Phascolomys* in the family Phascolarctidæ.

4. I agree with Weber and Winge that there should be only two families, one for the Phalangers, and one for the Koala and Wombat; and there are characters of sufficient importance to place each of the animals in the latter in a separate subfamily. My views are tabulated thus:—

Family Phascolarctidæ.
Subfamily 1. Phascolarctinæ.
2. Phascolomyinæ.

Family Phalangeridæ.
Subfamily 1. Phalangerinæ.
Phalanger, Trichosurus.
Subfamily 2. Pseudochirinæ.
Pseudochirus.

5. If one simply enumerates characters and strikes a balance he will obtain one form of classification, but if he considers each feature and tries to detect the part it plays in the animal œconomy his results will be quite different. They will lead him to place the Koala and Wombat in the same family.

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